Variation and Population Structure of the Tourmaline Sunangel, *Heliangelus exortis exortis* (Aves, Trochilidae)

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ABSTRACT

The nominate form of the polytypic Andean hummingbird the Tourmaline Sunangel, *Heliangelus exortis exortis,* exhibits dramatic variation in a female polychromatism of throat iridescence within and among populations that has not heretofore been appreciated. An analysis of the geographic population structure of samples referable to *H. e. exortis* was conducted to determine the biological status and historical process of differentiation of polychromatically differentiated samples. Geographic variation in additional color and six mensural characters is discordant within and between the sexes. The polychromatism shows both regular and mosaic patterns of geographic varia-

tion. Geographic patterns of variability in the polychromatism do not appear to result from increased variability in putative zones of hybridization between differentiated populations. No character breaks that might indicate noninterbreeding parapatric forms were noted. It is concluded that *H. e. exortis* comprises a single biological entity and taxon within the polytypic *H. exortis* complex. The evolutionary origins of the complex pattern of geographic variation in *H. e. exortis* are discussed. I suggest that biological attributes, in addition to potential geographic barriers, are necessary for a full understanding of the geographic differentiation seen in *H. e. exortis*.

INTRODUCTION

There are few detailed studies of the geographic population structure of Andean birds (Vuilleumier, 1968, 1980a, 1980b, 1984; Graves, 1982). These studies have been aimed primarily at reconstructing the course of geographic speciation by describing geographic variation in terms of Mayr's (1959, 1963)

categories of isolates, continua (clines and related phenomena), and secondary contact. There are also classes of geographic variation that do not fit these categories but nevertheless manifest striking patterns. This is especially true in topographically complex mountain systems and oceanic archipelagoes.

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Unusual forms of geographic variation recorded in these regions include changes in sexual dimorphism, sex-limited variation, and mosaic, nonclinal variation (Mayr, 1942). These complex patterns suggest biological as well as extrinsic factors as causal agents of geographic variation, and are of general interest for understanding the full range of factors that promote geographic differentiation and speciation.

Because of great interest in their nectar-feeding habits, hummingbirds are becoming one of the better known avian families from the standpoint of ecology and behavior. This knowledge has additional application in studies of the biological basis of geographic differentiation, of which hummingbirds in the topographically complex Andes provide many dramatic examples (Zimmer, 1951a, 1951b, 1952). However, studies of hummingbird systematics have lagged far behind knowledge of their feeding ecology and behavior.

While conducting a survey of geographic variation and speciation patterns in Andean hummingbird genera, I found an unusual form of color variation in members of the genus *Heliangelus*. Females of several species exhibit dramatic variation in the development of the highly iridescent throat, or "gorget," characteristic of males (Bleiweiss, MS). This "polychromatic" variation is particularly pronounced within and among populations of the nominate form of the polytypic species *Heliangelus exortis,* the Tourmaline Sunangel. Samples from the central section of the Central and Eastern Cordilleras of Colombia show a range of variation from a noniridescent to a fully iridescent gorget similar to males, whereas samples from southern Colombia have only discrete noniridescent and fully iridescent male-like morphs. In contrast, the polychromatism is rare or absent in samples from the eastern slopes of the Andes in Ecuador.

Intraspecific sex-limited variation and variation in sexually dichromatic features are both rare phenomena in birds. The geographic population structure of *Heliangelus e. exortis* is therefore of great interest for (1) ascertaining whether *H. e. exortis* should be considered a single species and (2) gaining insight into the process of differentiation in

this exceptional form. The present paper treats geographic variation in the female polychromatism in conjunction with variation in other color and mensural characters to examine these questions.

ACKNOWLEDGMENTS

TAXONOMY OF THE *HELIANGELUS EXORTIS* COMPLEX

Hummingbirds of the genus *Heliangelus* Gould, 1848, are endemic to mid-elevations (1500–3000 m) of the Andes from Venezuela to Bolivia. Current taxonomic treatments recognize seven species in the genus, some of which are highly polytypic (Peters, 1945; Meyer de Schauensee, 1966). The Tourmaline Sunangel, *Heliangelus exortis,* is currently treated as a polytypic species comprised of a nominate form with violet-chinned and rose-throated males occurring in the three Andean ranges of Colombia south through the eastern slope of the Ecuadorian Andes, and two apparently allopatric forms with orange-throated males, *H. e. micraster* and *H. e. cutervensis,* in the Andes of southwestern Ecuador and northern Peru, respectively (Meyer de Schauensee, 1966). A number of characteristics support the conclusion that *H. e. exortis* and the orange-throated forms are closest relatives in *Heliangelus* (Zimmer, 1951b; Fitzpatrick, Willard, and Terborgh,

TABLE 1

Distribution and Sample Size for *Heliangelus exortis exortis* Specimens Examined

		Cordillera				
Locality	Pooled[a]	West	Central	East[b]	Adults	Immatures
1. El Peñón	A	—	—	West	1	—
2. La Aguadita	A	—	—	West	1	—
3. El Roble	A	—	—	West	6	1
4. Fusugasugá-Silvania	A	—	—	West	4	—
5. Hacienda Zuliaba	—	—	East	—	7	1
6. Santa Elena	—	—	East	—	2	—
7. Páramo de Sonsón	—	—	West	—	6	2
8. El Zancudo	B	—	West	—	17	1
9. Santa Isabel	B	—	West	—	1	1
10. Laguneta	—	—	West	—	43	15
11. Toche; Tolima	—	—	West	—	7	6
12. Puracé	—	—	West	—	1	—
13. Coconuco	—	—	West	—	1	—
14. Paletará	—	—	West	—	2	—
15. Almaguer	—	—	West	—	6	3
16. Hacienda La Ilusión	—	West	—	—	8	1
17. La Florida	C	East	—	—	1	—
18. Coast Range	C	East	—	—	3	—
19. Cerro Munchique	C	East	—	—	17	1
20. Munchique-El Tambo	C	East	—	—	2	1
21. Tijeras-Moscopán	—	—	East	—	5	—
22. Guanderal	D	—	—	East	3	—
23. Cerro Pax	D	—	—	East	8	5
24. Papallacta	E	—	—	East	7	—
25. Cuyujua	E	—	—	East	2	1
26. Baeza	E	—	—	East	3	—
27. Volcán Sumaco	—	—	—	Isolated peak	10	1
28. San Antonio	F	—	—	East	1	—
29. Ambato	F	—	—	East	1	1
30. Baños	F	—	—	East	6	1
31. Volcán Tungurahua	F	—	—	East	4	—
32. Planchas	—	—	—	East	—	2
33. Corazón	—	—	—	West	—	1

[a] Letters A–F designate pooled localities used for analysis of geographic variation.

[b] East and west designations under each Cordillera refer to the slope of the range.

1979; Bleiweiss, in prep.). Each can be distinguished from most sympatric congeners by the absence of a white pectoral band, and uniquely, by white female throat feathers and under-tail coverts in both sexes. The Purple-throated Sunangel, *H. viola,* also lacks a white pectoral band and may be closely related to *H. e. exortis* (Chapman, 1926). However, *H. viola* is sympatric with the orange-throated members of the *H. exortis* complex and is thus a distinct species. In my analysis, I define *H. e. exortis* as all rose-throated populations of the *H. exortis* complex.

MATERIALS AND METHODS

The present study is based upon 230 specimens from six museum collections; American Museum of Natural History, New York (AMNH), Academy of Natural Sciences, Philadelphia (ANSP), Carnegie Museum of Natural History, Pittsburgh (CAR), Museum of Comparative Zoology, Cambridge (MCZ), Louisiana State University Museum of Natural History (LSUMZ), and the National Museum of Natural History, Washington D.C. (USNM). I used all specimens with adequate
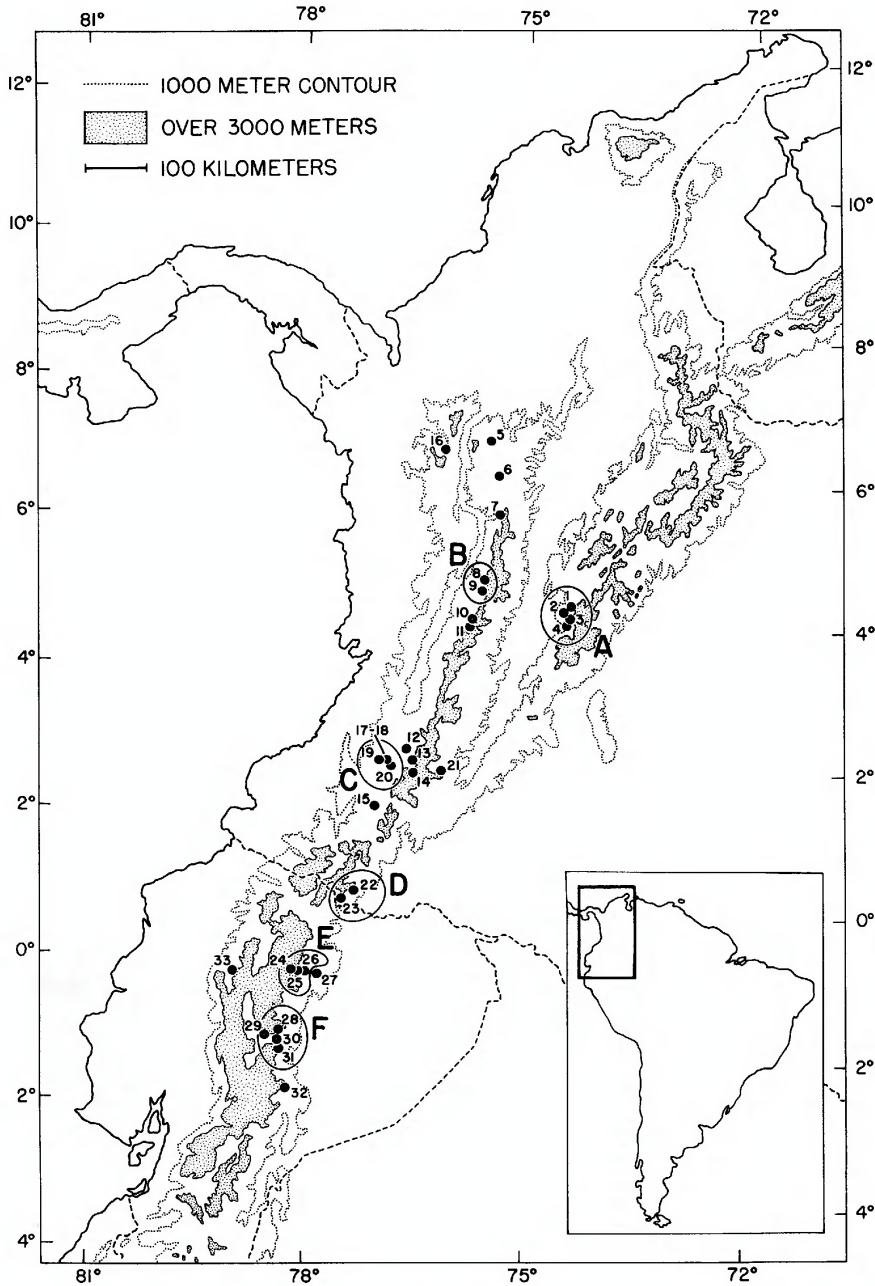
FIG. 1. Geographic distribution of *Heliangelus exortis exortis* specimens examined. Locality numbers are identified in table 1. Letters A–F indicate localities pooled for the analysis of geographic variation (see Appendix 1).

locality data from throughout the range of *H. e. exortis* (table 1, figure 1, see Appendix 1: Specimens Examined).

Study skins were aged and sexed by external characters since gonadal data were noted on the labels of only two specimens. Immatures were distinguished by the presence of corrugations on the culmen, lacking in adults (Ortiz-Crespo, 1972). Older immatures, recognized by their few bill corrugations, are

TABLE 2

Geographical Variation in Color Characters in *Heliangelus exortis exortis*[a]

	Population[b]	Male Throat	Female Throat		Under-tail Coverts
			Classes	Nonglittering	
A	Bogotá region	R	I–IV	w	w
5	Hacienda Zuliaba	R	II/IV	b	Faintly b
6	Santa Elena	R	–	–	b
7	Páramo de Sonsón	R	II/IV	b	b
B	El Zancudo, Santa Isabel	R	I–IV	b	b
10	Laguneta	R	I–IV	b	b
11	Toche	R	II/IV	b	b
12	Puracé	R	–	–	b
13	Coconuco	R	–	–	Faintly b
14	Paletará	R	IV	–	Faintly b
15	Almaguer	R	I/IV	w	w, b
16	Hacienda La Ilusión	R	IV	b	Faintly b
C	Cerro Munchique	R	II/IV	b	b
21	Tijeras-Moscopán	R	I/IV	w, b	w, b
D	Guanderal, Cerro Pax	R	I/IV	w	w
24–31	Eastern Andes of Ecuador	R	I	w	w
32	Planchas	–	I/S(?)	w	w
33	Corazón	–	IV	–	w

[a] Adults and immatures.

[b] Populations labeled as in table 1 and figure 1.

[c] Symbols for characteristics of gorget: R = glittering rose with violet chin; S = scaled, white with glittering rose edge; w = white; b = bicolored, white with a shining green to dusky mark; w, b = both white and bicolored conditions present.

Female throat class symbols described in Materials and Methods.

similar to adults in throat color (Bleiweiss, 1983), and are included in evaluating patterns of geographic variation in coloration. Immature hummingbirds do differ from adults in mensural characters (Stiles, 1983). I include measurements for only 2 of special interest from among the 42 examined since most localities had few immatures (table 1). Criteria for distinguishing the sexes based upon measurements and body coloration were developed in Bleiweiss (1983), and the results were utilized for this study. Females differ from males in having a lighter green body plumage and tan bellies, and are consistently smaller in two dimensions, length of the first primary and length of the outer tail feather (rectrix 5); a length of 45.5 mm for both measurements was found to separate the sexes.

To describe variation in the brilliance of iridescence, I use Greenewalt's (1960) terms "glittering" and "shining" to refer to iridescent reflections of high and low brilliance,

respectively. The female polychromatism consists of variation in glittering throat feathers which I quantified by the method devised by Bleiweiss (1983). Individuals were divided into four classes based upon the number of glittering throat feathers; class I = 0; class II = 1–17; class III = 21–28; class IV = 31–50+. Classes II and III have a mixture of glittering and nonglittering feathers while classes I and IV generally have only nonglittering or glittering feathers, respectively.

For the analysis of population structure, six measurements were taken on study skins judged to be adults: length of exposed culmen (EC), length of culmen from flange of the nasal operculum (CF), length of first primary (FP), chord length of unflattened wing (WB), and lengths of inner (IT) and outer (OT) tail feather (Baldwin et al., 1931).

The mapping of collecting localities was accomplished with the aid of recently compiled gazetteers of ornithological collecting
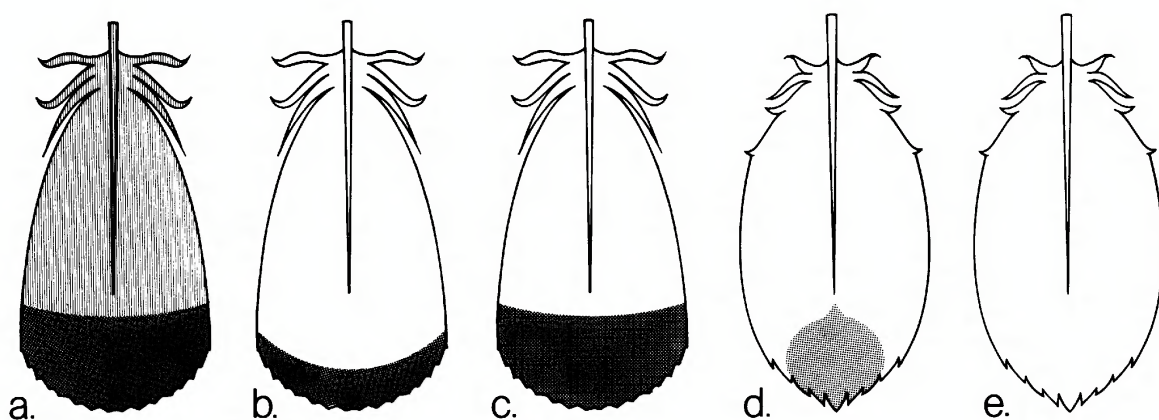
FIG. 2. Throat feather types of male and female *Heliangelus e. exortis*. From left to right: (a) glittering rose feather from adult male; (b) white, fringed glittering rose feather from immature "female" from Planchas, southern Ecuador; (c) white, glittering rose feather from adult female; (d) bicolored feather from adult female; (e) fully white feather from adult female.

localities in South America (Paynter and Traylor, 1977, 1981). Museum materials from specific localities represent small, sometimes temporally heterogeneous collections, and are referred to here as samples. In the statistical analysis of geographic variation, some geographic samples were pooled as noted in table 1 and figure 1. Groupings of geographic samples were based upon close geographic proximity and absence of an obvious geographic barrier between them (Vuilleumier, 1968). The samples were homoscedastic by F-max (Sokal and Rohlf, 1981) and met other assumptions for parametric ANOVA. I therefore used one-way ANOVA with *a posteriori* Scheffé contrasts to analyze patterns of geographic variation in the six measurements taken on adults. All male samples ≥ five and female samples ≥ four were included in the analysis.

VARIATION IN COLOR CHARACTERS

Table 2 summarizes geographic variation in color characteristics for each sex. The variation in throat feather color patterns is shown in figure 2. Males have glittering violet chins and rose throats at all localities. There is also one atypical immature specimen (fig. 2b) labeled as a male (LSUMZ 82902) from Planchas, Ecuador (locality 32), at the southern-

most known limit of rose-throated *H. e. exortis*. The throat feathers of this individual are white with narrow glittering rose edges, giving the throat a scaled appearance. This condition differs from all other immature male gorgets, which are similar to adults in color but reduced in extent. The sex of this specimen is problematical since the gonads were greatly reduced in size (1 × 1 mm). Immature hummingbirds have longer wings than adults so the measurements of this specimen are certainly more typical of females (FP = 42.8; OT = 41.1). I judge this specimen to be a female.

Adult female samples vary dramatically in throat class frequencies, from highly variable (I–IV) in the central section of the Central and Eastern Cordilleras of Colombia (localities A, B, and 10), to two pronounced classes (I and IV) at their southern end (localities 14, 15, 21, and D), to predominantly the non-iridescent class (I) on the eastern slope of the Andes in Ecuador (localities 24–31); one of two immature females from the southernmost collection in Planchas (locality 32) lacks throat iridescence.

Only a single immature specimen, with a fully developed gorget (count 40), has been collected in western Ecuador, labeled "lower west side of Corazón," west of Quito. This specimen was collected by Goodfellow and Hamilton in 1898, and was subsequently de-

scribed by Oberholser as a separate taxon *Heliangelus exortis soderstromi* (Oberholser, 1902). Oberholser believed the specimen to be a male. However, Chapman (1917) correctly surmised it to be a female, a determination I corroborated by measurements (FP = 45.2; OT = 42.2). Since the majority of immature and adult females from eastern Ecuador lack throat iridescence, this unique specimen from western Ecuador suggests differentiation of *H. e. exortis* between the Eastern and Western Cordilleras of Ecuador.

However, the accuracy of the collecting locality given for this specimen can be questioned, as Chapman (1917, 1926) noted. Several hummingbird species restricted to the eastern or western slopes of the Andes in Ecuador were reported from the opposite side of the Andes in the Quito region in early collections such as those of Goodfellow and Hamilton (see Oberholser, 1902 for examples). This situation may have resulted from inaccurate collecting information supplied by native collectors who were extremely active in the Quito region (Chapman, 1926) and who were employed by Goodfellow (Goodfellow, 1901). Chapman (1917) stated that the type of *H. e. soderstromi* appeared to be a native-made skin. Thus, the true geographic origin and potential evolutionary significance of this specimen remain in doubt.

Aside from polychromatic variation, only two other plumage characters vary: nonglittering throat feathers of females, and the under-tail coverts of both sexes. In Colombia, the nonglittering throat feathers are bicolored, white with a shining green to dusky terminal dot (fig. 2d) in samples from the Western and Central Cordilleras south through Laguneta (locality 10), and pure white (fig. 2e) in the southernmost sample from the Central Cordillera in Almaguer (locality 15), and in all samples in the Eastern Cordillera southward into eastern Ecuador. While each sample has a characteristic pattern, there is some variation within them. Single individuals with large numbers of bicolored throat feathers occur at the "white" localities of El Peñón (locality 1), Tijeras (locality 21), and Baeza (locality 26), while there is also one individual with pale dusky markings at El Zancudo (locality 8), a "bicolored" locality.

Color variation in the under-tail coverts is similar to nonglittering throat feathers, ranging from bicolored to pure white. Geographic variation in under-tail coverts usually parallels that of nonglittering throat feathers, with bicolored under-tail coverts in samples with bicolored throat feathers and white under-tail coverts in samples with white throat feathers (table 2). The type of *H. e. soderstromi,* which has a fully rose throat, has white under-tail coverts.

There is some evidence for intermediacy in the color and correlation of these two characters in the region between Laguneta (locality 10) and Cerro Pax (locality D): intervening samples from both slopes of the Central Cordillera in its southern section (localities 12–15, 21) are highly variable or intermediate. On the west slope, the single male from Puracé (locality 12) had pronounced dusky centers on the under-tail coverts, closest in color to samples to the north. Specimens south of Puracé from Coconuco, Paletará, and Almaguer (localities 13–15), were fainter, or pure white like specimens farther south (locality D southward). Specimens from the eastern slope in Tijeras (locality 21) show similar variation and in addition, show both white and bicolored class I throats. Furthermore, the correlation between throat and under-tail covert coloration appears to break down in this region since Tijeras females have various combinations of the two throat and under-tail covert conditions (table 2).

GEOGRAPHIC VARIATION IN MEASUREMENTS

Table 3 presents descriptive statistics of the six mensural characters for adults of both sexes. Table 4 presents a summary of the results of the one-way ANOVA with Scheffé contrasts for the six measurements for adults of both sexes. In males, five measurements showed significant heterogeneity among means. However, the Scheffé contrasts among means indicate that this is due largely to the small size of males from the Cerro Munchique region of the Western Cordillera (localities 17–20 and C). Males from the Cerro Munchique region differed significantly from samples from three prominent massifs: Volcán Sumaco (locality 27), Hacienda La Ilusión (locality 16), and the Nevado de Tolima

TABLE 3

Means and Standard Deviations (in Millimeters) of Six Mensural Characters for Adult Males (A) and Females (B)

Loc.	EC Mean ± SD (N)	CF Mean ± SD (N)	FP Mean ± SD (N)	WB Mean ± SD (N)	IT Mean ± SD (N)	OT Mean ± SD (N)
			Males (A)			
A	15.14 ± 0.70 (5)	17.19 ± 0.28 (5)	47.34 ± 1.30 (5)	63.46 ± 2.70 (5)	32.95 ± 1.64 (5)	49.37 ± 2.39 (5)
5	16.00 ± 0.68 (2)	18.85 ± 0.47 (2)	47.43 ± 1.28 (3)	64.53 ± 1.65 (3)	34.10 ± 0.06 (2)	46.58 (1)
6	15.70 ± 0.88 (2)	18.38 ± 0.51 (2)	46.21 ± 0.37 (2)	62.78 ± 1.58 (2)	33.53 ± 1.06 (2)	46.77 ± 0.27 (2)
7	15.93 ± 0.46 (3)	18.62 ± 0.54 (3)	48.26 ± 1.52 (4)	65.07 ± 1.91 (4)	33.11 ± 1.41 (5)	49.47 ± 1.05 (5)
B	15.94 ± 0.53 (10)	18.81 ± 0.36 (10)	47.20 ± 1.48 (10)	63.38 ± 2.90 (10)	33.09 ± 1.30 (10)	47.19 ± 1.26 (9)
10	15.89 ± 0.56 (22)	18.67 ± 0.41 (22)	48.02 ± 1.26 (22)	64.58 ± 2.65 (22)	33.11 ± 1.59 (22)	47.91 ± 1.31 (22)
11	15.87 ± 0.58 (6)	18.50 ± 0.44 (6)	47.70 ± 0.77 (5)	64.13 ± 0.94 (5)	33.67 ± 1.40 (5)	47.81 ± 1.72 (6)
12	15.3 (1)	18.3 (1)	49.1 (1)	66.3 (1)	31.7 (1)	49.8 (1)
13	15.2 (1)	18.0 (1)	48.2 (1)	65.6 (1)	34.3 (1)	49.2 (1)
14	15.4 (1)	18.4 (1)	49.8 (1)	67.3 (1)	33.7 (1)	50.5 (1)
15	14.84 ± 0.42 (2)	18.02 ± 0.11 (2)	49.63 ± 0.34 (4)	65.48 ± 1.21 (4)	35.04 ± 0.89 (4)	51.02 ± 2.25 (4)
16	16.32 ± 0.59 (6)	18.63 ± 0.60 (6)	47.92 ± 1.54 (5)	65.07 ± 1.57 (5)	33.77 ± 0.74 (5)	48.12 ± 2.44 (6)
C	15.19 ± 0.61 (17)	17.88 ± 0.59 (17)	46.96 ± 1.17 (15)	63.39 ± 1.60 (15)	33.12 ± 1.06 (16)	46.96 ± 1.69 (15)
21	15.70 ± 0.59 (2)	18.34 ± 0.03 (2)	46.93 ± 1.00 (2)	64.34 ± 1.36 (2)	34.18 ± 1.09 (2)	47.50 ± 0.14 (2)
D	15.20 ± 0.51 (4)	18.58 ± 0.44 (4)	48.52 ± 1.51 (5)	65.94 ± 2.94 (5)	34.04 ± 3.46 (2)	48.92 ± 0.13 (2)
E	15.80 ± 0.52 (7)	18.64 ± 0.54 (7)	49.25 ± 1.52 (6)	67.09 ± 2.05 (6)	33.97 ± 1.16 (7)	50.71 ± 1.64 (7)
27	15.34 ± 0.39 (8)	18.34 ± 0.26 (8)	49.63 ± 0.87 (7)	67.75 ± 1.12 (7)	34.41 ± 2.09 (8)	49.78 ± 1.02 (7)
F	15.57 ± 0.55 (8)	18.42 ± 0.63 (8)	47.75 ± 1.05 (7)	65.69 ± 2.16 (7)	34.21 ± 1.05 (8)	48.67 ± 1.05 (8)
			Females (B)			
A	15.16 ± 0.64 (7)	17.98 ± 0.35 (7)	43.33 ± 0.56 (7)	59.18 ± 0.76 (7)	31.72 ± 1.57 (6)	42.22 ± 1.52 (4)
5	17.28 ± 0.59 (4)	19.54 ± 0.39 (4)	43.42 ± 0.67 (2)	58.99 ± 0.95 (2)	32.28 ± 1.67 (4)	41.09 ± 0.33 (2)
6	—	—	—	—	—	—
7	15.6 (1)	18.6 (1)	43.2 (1)	58.9 (1)	—	—
B	16.45 ± 0.67 (7)	19.26 ± 0.49 (7)	41.09 ± 1.75 (6)	56.29 ± 2.10 (6)	31.58 ± 0.76 (7)	40.37 ± 0.59 (6)
10	16.31 ± 0.61 (21)	19.04 ± 0.60 (21)	43.25 ± 0.81 (20)	58.14 ± 1.59 (17)	31.92 ± 1.65 (20)	41.41 ± 1.93 (19)
11	15.7 (1)	18.4 (1)	42.2 (1)	57.2 (1)	30.2 (1)	39.6 (1)
12	—	—	—	—	—	—
13	—	—	—	—	—	—
14	15.5 (1)	18.7 (1)	44.5 (1)	60.5 (1)	—	—
15	15.58 ± 1.10 (2)	18.71 ± 1.12 (2)	44.28 ± 0.20 (2)	59.04 ± 0.93 (2)	31.71 ± 0.61 (2)	41.88 ± 0.42 (2)
16	17.22 ± 0.35 (2)	19.11 ± 0.30 (2)	43.1 (1)	59.2 (1)	32.45 ± 2.71 (2)	40.82 ± 1.99 (2)
C	16.12 ± 0.52 (6)	18.63 ± 0.66 (6)	43.24 ± 1.78 (5)	58.60 ± 1.80 (5)	31.46 ± 1.66 (6)	40.27 ± 1.37 (6)

TABLE 3—(*Continued*)

Loc.	EC Mean ± SD (N)	CF Mean ± SD (N)	FP Mean ± SD (N)	WB Mean ± SD (N)	IT Mean ± SD (N)	OT Mean ± SD (N)
21	16.35 ± 0.61 (3)	19.35 ± 0.49 (3)	42.64 ± 0.61 (3)	57.57 ± 0.73 (3)	30.42 ± 1.14 (3)	40.53 ± 1.02 (3)
D	15.96 ± 0.25 (6)	18.82 ± 0.45 (6)	42.99 ± 2.20 (5)	59.82 ± 1.79 (5)	33.17 ± 1.51 (4)	40.84 ± 1.59 (6)
E	15.65 ± 0.50 (5)	18.39 ± 0.44 (5)	44.76 ± 1.04 (5)	61.36 ± 1.00 (5)	31.81 ± 0.84 (3)	42.88 ± 1.54 (5)
27	15.31 ± 0.80 (2)	18.45 ± 0.52 (2)	43.85 ± 0.07 (2)	61.02 ± 1.34 (2)	32.63 ± 2.02 (2)	41.61 ± 0.95 (2)
F	15.80 ± 0.46 (4)	19.09 ± 0.53 (4)	42.80 ± 1.29 (4)	59.01 ± 1.75 (4)	32.19 ± 1.02 (4)	40.93 ± 1.48 (4)
32[a]	—	17.7 (1)	42.8 (1)	58.6 (1)	33.1 (1)	41.1 (1)
33[b]	14.7 (1)	—	45.2 (1)	61.5 (1)	35.0 (1)	42.2 (1)

[a] Immature with scaly throat iridescence.
[b] Immature previously described as *H. e. soderstromi*.
Abbreviations for characters explained in Materials and Methods.

region (localities B and 10). There was no significant differentiation among other localities within the main portion of the range. Sample sizes for females were smaller and the pattern less consistent than for males. Four of six characters showed significant heterogeneity among means. In contrast to males, females from El Zancudo (locality B) and Laguneta (locality 10) are most divergent, differing significantly from localities in the Eastern Cordillera of Colombia and the eastern slopes of the Ecuadorian Andes.

POPULATION STRUCTURE

The complex population structure that emerges for *H. e. exortis* is indicated by at least four different patterns among the various characters:

(1) Differences between the sexes in geographic variation of color and mensural characters. Males do not vary in any throat color feature, whereas females are highly variable in throat coloration within and between localities. In mensural characters, males from the Cerro Munchique region (locality C) in the Western Cordillera of Colombia are most distinctive (smallest) in five characters. Females from Cerro Munchique are not significantly different from females from any other locality. Rather, females from the Central Cordillera (localities B and 10) are the most distinct, differing from four (B) and three (10) other localities, respectively.

(2) Lack of concordance in the geographic variation among color and between color and mensural characters within females. Among color characters, changes in throat class frequencies are not paralleled by changes in nonglittering throat feathers (white or bicolored). For example, the white feather condition is observed throughout the Eastern Cordillera of Colombia through the eastern slope of the Andes in Ecuador, whereas the throat class frequencies change dramatically from highly variable (I–IV), to two discrete classes (I and IV), to predominantly class I.

No samples in the Eastern Cordillera from the Bogotá region (locality A) through the east Andean slope in Ecuador differed significantly in mensural characters even though there is a dramatic change in throat color

TABLE 4

Results of One-Way ANOVA for Geographic Variation in Mensural Characters in
Heliangelus exortis exortis

Character	Significantly Different					
	Males			Females		
Length of exposed culmen	16	>	C	B, 10	>	A
Length of culmen from flange	B, 10	>	C	B, 10	>	F
Length of first primary	27	>	C	B	<	A, 10, E
Length of wing cord	27	>	C	B, 10	<	E
Length of outer tail feather	E	>	C, B	ns		

ns = not significantly different.

Characters showing significant heterogeneity among means at 0.05 level of significance are listed on the left-hand side of the table. Inner tail feather (IT) for both sexes, and the outer tail feather (OT) of females show no significant variation. Locality numbers and pooled locality letters refer to table 1. Symbols indicate size relationships.

classes present. Conversely, females from El Zancudo differ from females in the Eastern Cordillera (locality A) in several measurements but both show a highly variable polychromatism (classes I–IV).

(3) Regular patterns of geographic variation in single characters in both sexes. Both nonglittering female throat feathers and under-tail coverts in both sexes vary together in a clear geographic pattern. Bicolored nonglittering throat feathers in females and bicolored under-tail coverts in both sexes are found in the Western and Central Cordilleras south to Almaguer (locality 15), whereas these features are exclusively white in the Eastern Cordillera south through the east Andean slope in Ecuador.

(4) Mosaic patterns of geographic variation in the polychromatism. There is progressive loss of polychromatic color classes from north to south in the best sampled region, from the central section of the Central and Eastern Cordilleras of Colombia south into Ecuador. This pattern constitutes a regular loss of variability in terms of the number of color classes, but shows no inherent directionality in the color classes present. Thus it does not conform to the classical definition of a cline (Mayr, 1963). Moreover, while increased phenotypic variability has often been documented in zones of secondary contact between two differentiated populations (Mayr, 1963; Short, 1969; Gill, Stokes, and Stokes, 1973; Endler, 1977), high variability (classes I–IV) in polychromatic samples does not appear to result from hybridization between

populations in secondary contact. The variable sample from Bogotá represents the probable northern limit of *H. e. exortis* in the Eastern Cordillera and cannot be a contact region between two differentiated populations.

DISCUSSION

Regular patterns of geographic variation permit evaluation of the degree of genetic continuity and history of differentiation of geographically variable forms. Clinal variation provides evidence of the interplay of local differentiation and gene flow among intraspecific populations. Conversely, concordant breaks or step clines in the variation of one or more characters suggest a reduction or cessation of gene flow between populations, from which species status can be inferred in the absence of behavioral data on reproductive isolation. Concordant patterns of geographic variation among different characters and taxa can be correlated with physical environmental features that could serve as extrinsic barriers to gene flow.

The complex population structure of *Heliangelus e. exortis* is a combination of regular, but also nonconcordant and even nonclassical patterns of character variation that do not easily fit into the above categories. This complexity makes an evaluation of the genetic continuity and history of differentiation along traditional lines difficult. Moreover, the discordant patterns of geographic variation within and between the sexes make an analysis of differentiation based upon ex-

trinsic barriers to gene flow difficult, since different barriers have to be invoked to explain different characters and patterns within and between the sexes.

Clearly, the range of population structures with dramatic differentiation extends beyond the traditional classifications of clines, step clines, and distinct isolates. Although *H. e. exortis* presents an especially complex pattern, the paucity of detailed studies of population structure makes it difficult to assess how prevalent these cases are among birds. Such patterns are part of the broader range of phenomena that must be considered in studies of the forces promoting geographic differentiation. In lieu of these considerations, what can be said of the genetic continuity and history of differentiation in *H. e. exortis*?

There is no evidence to contradict the status of *H. e. exortis* as a single biological entity within the *H. exortis* complex. *Heliangelus e. exortis* does not show concordant regional differentiation which would indicate a significant reduction or cessation of gene flow and thus either incipient or completed speciation. Rather, there is little concordant differentiation between males and females or even among different characters within each sex. Such major features of differentiation as the presence of polychromatic populations in Colombia and nonpolychromatic populations in Ecuador are not paralleled by similar dichotomies in other female characters, or by males, whose plumage is remarkably uniform throughout the entire range of the taxon.

Positive evidence of gene flow as indicated by intergradation between differentiated populations is less clear from the available data. Intergradation in characteristics of the under-tail coverts and nonglittering throat feathers in the southern portion of the Central Cordillera of Colombia is suggested, but is based upon few specimens.

As for the origin of the pattern of differentiation, it is tempting to interpret the general lack of concordance in variation among characters as evidence that differentiation has occurred *in situ*. However, caution is needed in interpreting whether geographic differentiation is primary or secondary (Endler, 1977). Alternatively, intraspecific patterns of variation may be due to minor or fluctuating degrees of genetic discontinuity between populations resulting from the general topographic complexity of the Andean region. This could be caused or at least enhanced by historical changes in the continuity of Andean habitats, which are believed to have undergone repeated fractionation and rejoining during the Pleistocene (Vuilleumier and Simberloff, 1980). This complex history could be difficult to decipher from patterns of geographic variation alone.

The deep arid valley of the Río Magdalena is one barrier promoting differentiation between Andean adapted forms in the Eastern and Central Cordilleras of Colombia (B. S. Vuilleumier, 1971) and could be an extrinsic barrier promoting differentiation in *H. e. exortis*. Isolation across this barrier is implicated in the differentiation of populations into those with white under-tail coverts and throat feathers in the Eastern Cordillera of Colombia and Ecuador, and those with bicolored ones in the Western and Central Cordilleras of Colombia. Females from the central section of the Central Cordillera are most divergent in measurements from females in the Eastern Cordillera of Colombia, thus supporting the role of the Río Magdalena valley as an effective barrier to gene flow between these two populations.

The major dichotomy among females of polychromatic populations in Colombia and largely nonpolychromatic ones in Ecuador cannot be similarly explained. However, the similar high variability in polychromatic samples (classes I–IV) from the same latitude in the central section of the Central and Eastern Cordilleras of Colombia is noteworthy in light of the differentiation between these populations in other characteristics. These two populations do not appear to be in contact since the variable Eastern Cordillera samples (locality A) form the northern range terminus for *H. e. exortis* in the Eastern Cordillera with no obvious northern connection with the Central Cordillera, while to the south populations are characterized by morphic variation (classes I and IV). Given the apparent effectiveness of the Río Magdalena valley as a physical barrier, the similar high levels of polychromatic variation may have been derived independently or have been selectively maintained despite secondary isolation.

In addition to extrinsic environmental factors, biological attributes of the species also seem important for explaining the broader aspects of differentiation, including the non-concordant and nonclassical patterns of geographic variation. Adaptive intrapopulation color variation may result from the coarse-grained (*sensu* MacArthur, 1972) utilization of the environment by these small-bodied homeotherms; hummingbirds are known to carefully select microhabitats for the purpose of thermoregulation and foraging (Gass and Montgomerie, 1981). Moreover, when the sexes have very different ecological and demographic characteristics, one would expect this to produce sex-limited patterns of variation at several levels. The prevalence of pronounced sexual dimorphism in size and color in hummingbirds indicates that each sex is under some different selection pressures. These differences seem likely to produce different patterns of geographic variation in the two sexes as well.

The effectiveness of barriers also depends upon intrinsic biological properties (Mayr, 1963). Birds are generally considered to be more mobile than other vertebrates but there is much variation in sedentariness among different groups. Some of the most dramatic examples of microgeographic variation, including changes in the frequency of intra-population color variants, occur in several families of birds in which nectar is an important component of the diet (the Coerebidae, Wunderle, 1981; the Zosteropidae, Gill, 1973). Thus, nectar-feeding habits may be particularly conducive to geographic differentiation over short distances, such as is also seen in *H. e. exortis*.

Females of hummingbird species with characteristically bright plumage in both sexes ("bright monomorphic") differ from dull-colored females of dichromatic species in being territorial exploiters of nectar during the nonbreeding season (Wolf, 1975). I have argued elsewhere that feeding territoriality in females of bright monomorphic humming-birds suggests that females with plumage like males in polychromatic species are also territorial (Bleiweiss, 1983). Thus, geographic variation in the polychromatism may reflect corresponding variation in floral resources or ecological competitors that affect foraging be-

havior in *Heliangelus*. Similarity in these conditions across major river barriers may explain the lack of corresponding differentiation in the polychromatism. Other patterns, such as the differentiation of populations in several mensural and color characters between the eastern Andean chain and the Central and Western Cordilleras, could be proximally caused by isolation across intervening river valleys.

These speculations still require confirmation or rejection from field studies on the function of plumage coloration in humming-birds. However, the population structure of *Heliangelus exortis exortis* demonstrates the need to expand explanations of geographic differentiation beyond the role of extrinsic environmental features, to include hypotheses based upon the biological properties of the organism and the biological function of specific characters.

TAXONOMIC CONCLUSIONS

I consider *Heliangelus e. exortis* to comprise a single taxon. I recognize no new taxa based upon changes in the frequency of different female color classes, even when only one class is present, since color classes are morphologically similar over broad areas. I agree with Chapman (1917) and regard *H. e. soderstromi* as a junior synonym of *H. e. exortis* since the specimen on which *soderstromi* is based is obviously an iridescent female color form. The white under-tail coverts of this bird suggest its affinity with specimens from eastern Ecuador. Though it also has a rather short bill [table 3(B)], this is probably due to its immaturity. One of the two immatures from Planchas differs from males and females of other localities in its scaly throat feathering. This difference may be taxonomically significant. However, more material is needed to characterize this population and verify the proper sex of this specimen (female?).

Chapman (1917) noted the variation in nonglittering throat feathers but thought that the bicolored condition indicated immaturity. My data indicate that color differences in the nonglittering throat feathers and under-tail coverts exist among adult birds, and vary in a regular geographic pattern, with bi-

colored feathers found in populations of the Western and Central Cordilleras and white feathers in the Eastern Cordillera and the east Andean slope of Ecuador. The similar color variation from white to bicolored in both nonglittering throat feathers and under-tail coverts suggests that these characters are interdependent, so their concordant pattern does not seem sufficient to warrant taxonomic recognition in the absence of other highly correlated variation. More sampling is required from the critical southern section of the Central Cordillera of Colombia to determine the geographic pattern where bicolored and white forms are in apparent contact.

APPENDIX 1: SPECIMENS EXAMINED

Colombia: Locality A: AMNH 121632–34, 121636–39; ANSP 168270; LSUMZ 33621; USNM 255902–03. Hacienda Zuliaba: USNM 425771–78. Santa Elena: AMNH 133159–60. Páramo de Sonsón: USNM 436231–33, 436235–39. Locality B: AMNH 111686, 111688; ANSP 73749–50; CAR 70320–23, 70367–68, 70372–73, 70381–84, 70396, 70437. Laguneta: AMNH 111658, 111660, 111664, 111668–72, 111675, 111678–84; ANSP 153270–99, 153301–05, 153360, 153556, 153874; USNM 255905–06, 255908–09. Toche: ANSP 153306–15, 153317–19. Puracé: USNM 389240. Coconuco: ANSP 142594. Paletará: USNM 389242–43. Tijeras-Moscopán: USNM 389241, 446299–301, 446230. Almaguer: AMNH 115940, 115942–47, 185040, 255904. Hacienda La Ilusión: USNM 436240–46, 436247–48. Locality C: AMNH 109492–98; ANSP 129814, 142592–93, 144754–58; CAR 137296–98, 137327; LSUMZ 38574, 44665–66; USNM 446225–28. Locality D: ANSP 161991–93, 164796, 164798–802, 164804–10.

Ecuador: Locality E: AMNH 163096, 175971–73, 247236–37; USNM 174013–17, 180105–06. Volcán Sumaco: AMNH 175970, 185031–39, 185041. Locality F: AMNH 35540, 437688, 483691; ANSP 145523–32; LSUMZ 33621. Planchas: LSUMZ 82902–03. Corazón: USNM 174008.

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